ELSEVIER

Soil Biology & Biochemistry 37 (2005) 1419–1426

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Seasonal variations in enzyme activity and organic carbon in soil of a burned and unburned hardwood forest

R.E.J. Boerner*, J.A. Brinkman, A. Smith

Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 1735 Neil Avenue, Columbus, OH 43210, USA

Received 25 June 2004; received in revised form 16 December 2004; accepted 20 December 2004

Abstract

This study examined variations in soil organic C content and the activity of acid phosphatase, α-glucosidase, phenol oxidase, chitinase, and L-glutaminase in ultisols of burned and unburned areas in *Quercus*-dominated forests in Ohio, USA. The low intensity, prescribed fires were conducted in April 2001, with temperature 10 cm above the forest floor averaging 160–240 °C. Sampling was conducted throughout the six month growing season (May–October) of 2003, two years after the fire. Organic C content in these ultisols varied between 20 and 30 g C/kg soil, and varied little through the growing season, except for a late season increase to ~32 g C/kg soil in the burned areas. When enzyme activity was expressed per unit soil organic C, there was no statistically significant variation among sample dates in soil enzyme activity except L-glutaminase, which demonstrated a distinct maximum in activity in spring. Non-metric multidimensional scaling (NMS) ordination resulted in no clear separation of burned and unburned sample areas based on soil organic C and enzyme activity. When the growing season was divided into three segments (early spring, late spring/early summer, and late summer/early autumn), there was again a lack of separation between burned and unburned areas in the earlier two segments, whereas in the late summer/early autumn segment the burned and unburned areas were clearly separated on the basis of differences in soil organic C and L-glutaminase activity. As environmental factors (e.g. soil temperature, moisture) and substrate availability do not vary in parallel through the growing season in this region, seasonal patterns often differ among enzyme systems based on their predominant control mechanism. Sampling time during the growing season appears to have little effect on holistic judgments of fire effects based on soil enzymes, except under restrictive conditions.

Keywords: Acid phosphatase activity; α-Glucosidase activity; Phenol oxidase activity; Chitinase activity; L-glutaminase activity; Fire; Hardwood forest

1. Introduction

The history of the use of prescribed fire for forest management, restoration, and conservation dates to the 1940s, and is almost as long ago as the history of the policy and practice of fire suppression that led to the need for prescribed fire. In the late 1940s prescribed fire was adopted as an understory density and wildfire fuel management tool in coniferous forests in the southeastern US (Riebold, 1971). Since that time, the use of prescribed fire has grown to be continent-wide in extent and far more diverse in intent, with applications for purposes as diverse as wildlife conservation, wildfire hazard reduction, and ecosystem restoration. As the use of fire for restoration and conservation has grown, so has the need for robust, quantitative metrics of the effects of fire on the ecosystem as a whole, including soil quality and functioning.

Previous studies have demonstrated that soil biochemical parameters such as soil enzyme activities are sensitive indicators of stress on such ecosystems and have the potential to serve as robust measures of the health and sustainability of managed ecosystems (e.g. Bergstrom et al., 1998; Dick, 1994; Dick and Tabatabai, 1992). These enzymes serve as indicators of the activities of fungi, bacteria, and other soil organisms over periods of weeks prior to the soil being removed from the field. As such, they represent a holistic view of the acclimation response of the microbial assemblage to the suite of organic matter types and environmental conditions of the site over an ecologically-significant period of time.

* Corresponding author. Tel.: +1 614 292 6179; fax: +1 614 292 2030.
E-mail address: boerner.1@osu.edu (R.E.J. Boerner).

0038-0717/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2004.12.012

Fire often results in effects on organic matter and microbial community structure that can be detected by quantifying enzyme activity. For example, acid phosphatase activity, as an indicator of overall microbial activity, often decreases as a consequence of fire (e.g. Saa et al., 1993; Eivasi and Bayan, 1996; Boerner et al., 2000). Our previous studies of soil enzyme activities in forested ecosystems of southern Ohio (USA) demonstrated strong spatial patterns of variation within watersheds (Decker et al., 1999) and short-term effects of fire in some sites (Boerner et al., 2000). To date, however, we had not determined the degree to which these spatial and fire-induced variations were stable as soil microclimate and weather change through the cool, temperate growing season. Thus, the specific objectives of this study were to investigate (a) organic C content and activity of various enzymes variations through the growing season, and (b) the effects of a single, low intensity prescribed fire on organic C and enzyme activities as influenced by season of sampling.

2. Materials and methods

2.1. Study site and sampling design

The site of this study was located in Zaleski State Forest (82°22′W, 39°21′N) in Vinton County on the unglaciated Allegheny Plateau of southern OH, USA. The climate of the region is cool, temperate and continental with mean annual temperature and precipitation of 11.3 °C and 1024 mm, respectively (Sutherland and Hutchinson, 2003). The site was a block of approximately 140 ha of contiguous mixed-oak forest that developed following clear-cutting for charcoal production 100–150 years ago, and has not been managed or disturbed since that time (Sutherland and Hutchinson, 2003). The canopy was dominated by oak species (e.g. *Quercus alba*, *Quercus velutina*, *Quercus rubra*) and the subcanopy/understory by a combination of red maple (*Acer rubrum*), American beech (*Fagus grandifolia*) and black gum (*Nyssa sylvatica*).

The soils sampled in this study were predominantly Gilpin series silt loams (Ultisol: typic halpludult) formed in residuum and colluvium from Pennsylvanian age sandstones, siltstones, and shales (Boerner and Sutherland, 2003). These A horizons of these soils are strongly acidic (pH range 3.8–5.2), have low Ca:Al molar ratio (range 0.01–3.50), and this region is also subject to heavy chronic N deposition in precipitation (Boerner and Brinkman, 2003, 2004).

The study site was divided into four treatment units of 25–35 ha each, and treatment units were randomly allocated to four treatments: control, dormant season prescribed fire, thinning to pre-settlement basal area, and the combination of prescribed fire and thinning. We sampled each treatment unit for a full growing season prior to the imposition of treatments, and found no significant difference among the four treatment units in a range of physical, chemical, and biochemical soil properties (Boerner and Brinkman, 2004). The research described here took place in the control and prescribed fire units only, as the focus was on quantifying seasonality in these forests soils rather than assessing the full range of treatments. The effects of all four treatments one and four years after application on soil properties, vegetation, and wildlife are being analyzed as part of a national scale study replicated in thirteen areas across North America (National Fire and Fire Surrogates Network Study, www.ffs.fed.us) and will be published elsewhere in the near future.

Each watershed-scale treatment unit was stratified using a GIS-based integrated moisture index (hereafter, IMI) developed by Iverson et al. (1997) for this region. The IMI stratification was achieved through integration of elevation, aspect, hill shade profile, solar radiation potential, downslope flow accumulation, soil depth, soil water holding capacity, and curvature profile (Iverson et al., 1997). Areas occupying three IMI classes (xeric, intermediate, and mesic) were delimited within each treatment, and three 0.1 ha random, permanent sampling plots were established within each IMI class in each treatment unit ($N=9$ per treatment unit). For this study, only the sampling plots located in the intermediate IMI classes were used ($N=3$ per treatment unit), and all were located in midslope positions on SE or E facing slopes. In addition we restricted the sampling to the intermediate IMI class plots in order to focus on seasonality without confounding effects of landscape position. Analysis of the influence of landscape position and the interaction of landscape position and fire on soil properties based on 1–2 sampling dates/growing season are given by Decker et al. (1999), Boerner et al. (2000), and Boerner and Brinkman (2003, 2004).

The prescribed fire was conducted in April 2001, and maximum fire temperatures at 10 cm above the forest floor in the areas near we sampled were 160–240 °C (Iverson, unpublished data). This low intensity fire was designed to recreate natural dormant-season fires that characterized this system until fire suppression was introduced in the 1930s (Sutherland and Hutchinson, 2003).

From just before the deciduous trees came into leaf (mid-May) through litterfall (early October) of the 2003 growing season, soil samples were taken from each of the four corners of each sampling plot in the control and prescribed fire units. The four samples taken around each sample plot were separated by distances of 20–54 m, and sample plots were separated by random distances of 150–200 m. As previous studies of soil chemical and biochemical properties in this and neighboring sites have demonstrated that samples taken >10 m apart are spatially uncorrelated in soil organic matter content and microbial activity (Boerner and Brinkman, 2004), the four samples taken around a given sample plot were considered to be independent of each other. In addition, as the prescribed fire at this site was patchy in intensity and duration (Iverson, unpublished data),

each sample plot likely received a different and random fire treatment.

2.2. Soil sampling and laboratory analysis

After pushing aside unconsolidated leaf litter, samples of approximately 100 g of the top 15 cm of the $O_a + A$ horizon soil were taken at each corner on each date and returned to the laboratory under refrigeration. Samples on successive dates were always taken within 75 cm of those from the previous date. Soils were passed through a 2 mm sieve to remove coarse soil including stones and root fragments, and then analyzed for soil organic C content and the activity of five enzymes: phosphomonoesterase (acid phosphatase), chitinase, α-glucosidase, phenol oxidase, and L-glutaminase.

The first four enzymes were analyzed using methods developed by Tabatabai (1982), as modified by Sinsabaugh (Sinsabaugh et al., 1993; Sinsabaugh and Findlay, 1995). Subsamples of approximately 10 g of fresh soil were suspended in 120 ml of 50 mM NaOAc buffer (at pH 5.0 to best reflect the native soil conditions) and homogenized by rapid mechanical stirring for 90 s. To minimize sand sedimentation, stirring was continued while aliquots were withdrawn for analysis.

Acid phosphatase (EC 3.1.3.2), α-glucosidase (EC 2.2.1.20), and chitinase (EC 3.2.1.14) activities were determined using *p*-nitrophenol (*p*NP) linked substrates: *p*NP-phosphate for acid phosphatase, *p*NP-α-glucopyranoside for α-glucosidase, and *p*NP-glucosaminide for chitinase. Samples were incubated for 1 h (acid phosphatase, α-glucosidase) or 2 h (chitinase) at 20–22 °C with constant mixing. Following incubation, samples were centrifuged at $3000 \times g$ for 3 min to precipitate particulates. An aliquot of 2.0 ml of the supernatant was transferred to a clean, sterile tube, and 0.1 ml of 1.0 M NaOH was added to halt enzymatic activity and facilitate color development. Prior to spectrophotometric analysis at 410 nm each sample of the supernatant was diluted with 8.0 ml of distilled, deionized water.

Phenol oxidase (EC 1.14.18.1, 1.10.3.2) activity was measured by oxidation of L-DOPA (L-3,4-dihydroxyphenylalanine) during 1 h incubations at 20–22 °C. Following incubation, samples were centrifuged as above and analyzed at 460 nm without dilution. Parallel oxidations using standard horseradish peroxidase (Sigma Chemical) were used to calculate the L-DOPA extinction coefficient.

L-glutaminase (EC 3.5.1.2) was measured using a modification of the method described by Frankenberger and Tabatabai (1991a,b) designed to fit the soil characteristics of these acidic forest sites. Subsamples of approximately 0.5 g of soil were incubated with 0.9 ml of NaOAC buffer (pH 5.0) and 0.1 ml of 0.5 M L-glutamine at 37 °C for 30 min. After incubation, 4.0 ml of 100 ppm Ag_2SO_4 in 2.5 M KCl was added to each tube, and the tubes were centrifuged as above. NH_4^+ in the supernatant was determined colometrically using the method of Hamilton and Sims (1995). For all enzymes, we analyzed three analytical replicates of each subsample, and also performed substrate-free and soil-free controls for each sample to account for non-enzymatic substrate hydrolysis.

Organic C content was determined by Walkley-Black oxidation (Allison, 1965), using a conversion factor of 0.55 determined empirically for these forests (Boerner and Brinkman, 2004). The initial soil moisture and fresh/dry mass ratio of each soil sample was determined by drying 10–20 g of fresh soil at 65 °C to constant mass. We utilized this drying temperature to minimize the loss of volatile organics that can occur at 105 °C.

2.3. Data analysis

Soil enzyme activity was expressed on both soil mass and organic matter bases. Expressing activity on a soil mass basis reflects an ecosystem-level measure. The rate of consumption of organic substrates or production of enzymatic products can be calculated on an area basis (e.g. $g/m^2/day$) by combining activity expressed on a soil mass basis (i.e. μmol/g soil/h) with soil horizon depth and bulk density. Expressing activity on an organic matter basis (i.e. μmol/g organic C/h) reflects a microbial community property, as it expresses the nutritional status of the organic matter present from the perspective of the microbial community.

All response variables were either normally distributed or could be transformed to normality with a square root transformation. As successive samples were taken at distances apart that were greater than the range of spatial autocorrelation of microbial biomass and activity in this region (Morris, 1999), we considered this a completely randomized design with corners at which samples were taken nested within sample plots, and not as a repeated measures design. On each date $N = 12$ for each of the two treatment units.

Although this spatial design might initially be considered pseudoreplicated, applying randomly distributed, spatially-independent treatments to an array of sampling points which was determined to be spatially-independent prior to treatment and using pretreatment conditions as a covariate in subsequent analysis has proven to be an appropriate design for detecting environmental impacts (Stewart-Oaten and Murdoch, 1986; Underwood, 1994). Differences between treatment units on a given date were analyzed by one-way analysis of covariance, with samples nested within sample plots and pretreatment enzyme activities from the sampling done in 2000 as covariates (SAS, 1995).

To help visualize how soil organic C content and the activities of the five enzymes varied in relation to fire treatment and season, we ordinated the results by sample plot using non-metric multidimensional Scaling (NMS) (MjM Software Design, Gleneden Beach, OR). The initial NMS run was done using a set of initial parameters designed

to help determine the number of analysis dimensions (or axes) that would result in minimum stress in the covariance matrix. To prevent the distribution of relative activity levels among samples from being confounded by differences in absolute activity, final NMS analysis was done on a data matrix in which the values for each parameter among samples was standardized. Pearson product–moment correlations were used to determine relationships between soil properties and NMS axis scores.

3. Results

Soil organic C content averaged 23.5 g C/kg soil (±0.63, standard error of the mean) overall dates and sample plots. Organic C content did not differ between control and burned sample plots in May, early June, and July, and also did not vary significantly over the growing season in the control sample plots (Fig. 1). In contrast, organic C increased by 20–40% from July to September in the burned plots, and organic C content was significantly greater in the burned area than in the control in late June, August, September, and early October.

Acid phosphatase activity averaged 1.57 mmol/kg soil/h (±0.07) and 69.9 mmol/kg organic C/h (±2.0). On a soil mass basis, acid phosphatase activity was significantly

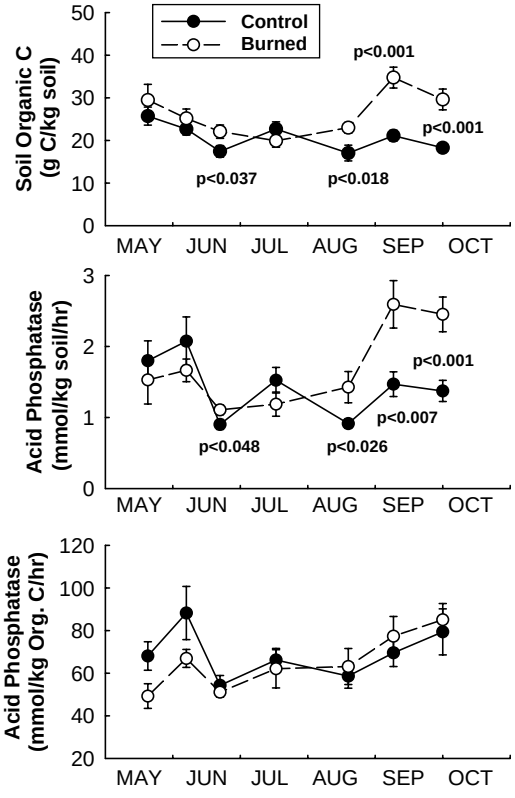

Fig. 1. Seasonal variations in soil organic C and acid phosphatase activity in soils of burned and unburned Ohio mixed-oak forests. Each point represents $N=12$. Where differences between burned and unburned sites was significant, the p value from one-way analysis of variance is given.

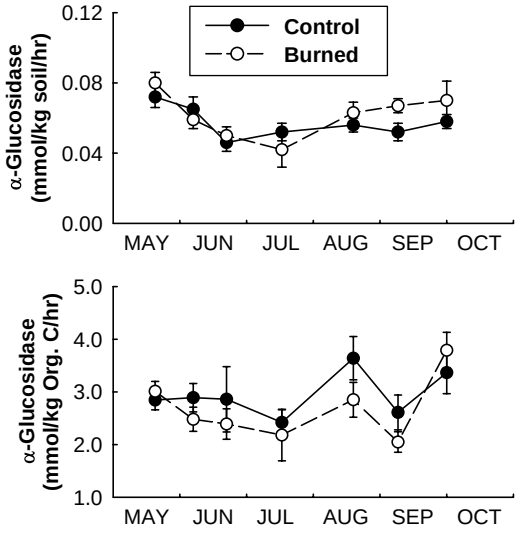

Fig. 2. Seasonal variations in α-glucosidase activity in soils of burned and unburned Ohio mixed-oak forests. Each point represents $N=12$. Where differences between burned and unburned sites was significant, the p value from one-way analysis of variance is given.

greater in soils from the burned plots than the unburned plots on the same dates as organic C content (Fig. 1). When estimated on an organic C basis, acid phosphatase activity differed neither between treatments nor among dates.

The activity of α-glucosidase averaged 0.06 mmol/kg soil/h (±0.01) and 2.7 mmol/kg organic C/h (±0.1), and there were neither significant effects of fire and nor significant seasonal variations in α-glucosidase activity (Fig. 2). The activity of L-glutaminase averaged 65.78 mmol/kg soil/h (±4.39) and 2876. 6 mmol/kg organic C/h (±171.6), and once again, there was no significant effect of fire on L-glutaminase activity, either on a soil mass or organic C basis (Fig. 3). There was,

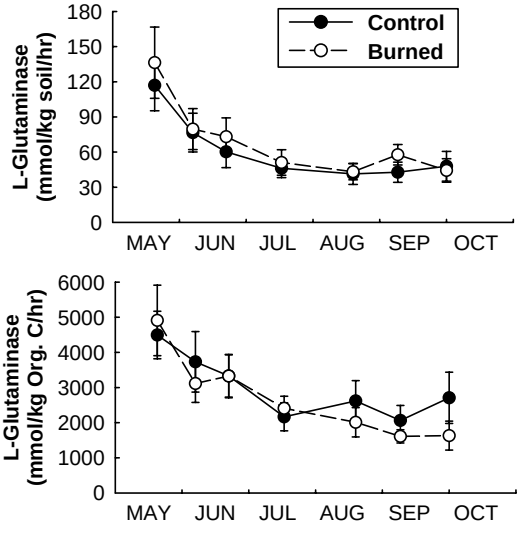

Fig. 3. Seasonal variations in L-glutaminase activity in soils of burned and unburned Ohio mixed-oak forests. Each point represents $N=12$. Where differences between burned and unburned sites was significant, the p value from one-way analysis of variance is given.

however, a significant seasonal effect on L-glutaminase activity with early spring maxima declining to stable minima by mid-summer (Fig. 3).

Chitinase activity averaged 0.13 mmol/kg soil/h (±0.01) and 5.8 mmol/kg organic C/h (±0.2). There were significant seasonal and fire effects on chitinase activity, which tended to be relatively higher in spring than in mid-summer (Fig. 4). During the spring maxima, chitinase activity was significantly greater in control soils than in soils from the burned plots. Chitinase activity increased again through late summer/early autumn, but only in the burned plots (Fig. 4). By early October, chitinase activity was significantly greater in soils from the burned plots than from control soils, on both soil mass and organic matter bases.

Phenol oxidase activity averaged 2.32 mmol/kg soil/h (±0.07) and 104.74 mmol/kg organic C/h (±3.14). Although there was no consistent seasonal pattern of variation in phenol oxidase activity, soil from burned sites had significantly greater phenol oxidase activity than did soils from unburned controls on four of seven dates on a soil mass basis and two of seven dates on an organic C basis (Fig. 5).

To visualize how soil organic C content and soil mass-based rates of organic C processing varied in a coordinated fashion to describe ecosystem function, we used NMS ordination to compare each sample plot and date in relation to fire. NMS arrayed the treatment/plot/date combinations along two axes that accounted for a total of 91.4% of the variance (Fig. 6). NMS Axis 1 (partial $r^2=0.424$) described a gradient that was negatively correlated with soil moisture and L-glutaminase activity and positively correlated with high phosphatase and chitinase activity. Thus, the samples from the moistest plots and with the greatest rate of amino acid hydrolysis were located at the lower end of NMS Axis 1, whereas those with the greatest phosphatase and chitinase activity were located at the upper end. NMS Axis 2 (partial $r^2=0.490$) described a gradient from that was positively correlated with Julian date and negatively correlated with organic C and L-glutaminase activity (Fig. 6).

The samples taken in spring (i.e. May, early June) generally ordinated on the lower half of NMS Axis 2, with burned plots located mostly in the center of NMS Axis 1 and unburned plots spanning the full range of NMS Axis 1 (Fig. 7). Thus, there was no clear separation between burned

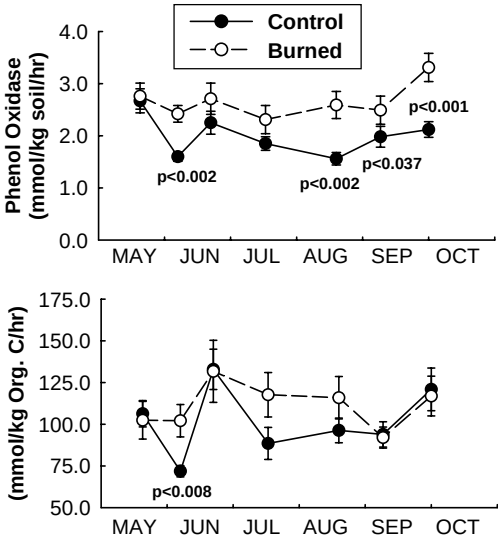

Fig. 5. Seasonal variations in phenol oxidase activity in soil of burned and unburned Ohio mixed-oak forests. Each point represents $N=12$. Where differences between burned and unburned sites was significant, the p value from one-way analysis of variance is given.

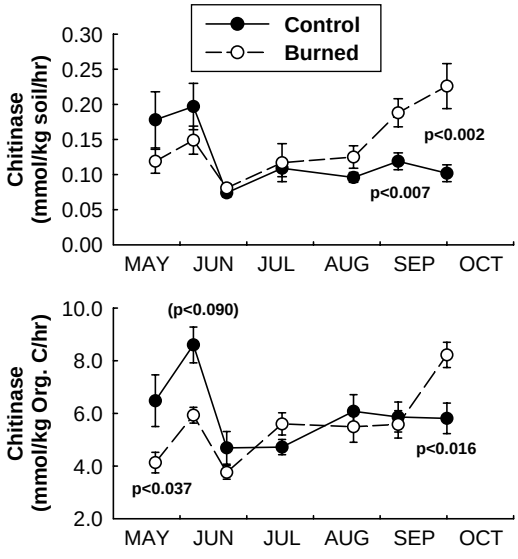

Fig. 4. Seasonal variations in chitinase activity in soils of burned and unburned Ohio mixed-oak forests. Each point represents $N=12$. Where differences between burned and unburned sites was significant, the p value from one-way analysis of variance is given.

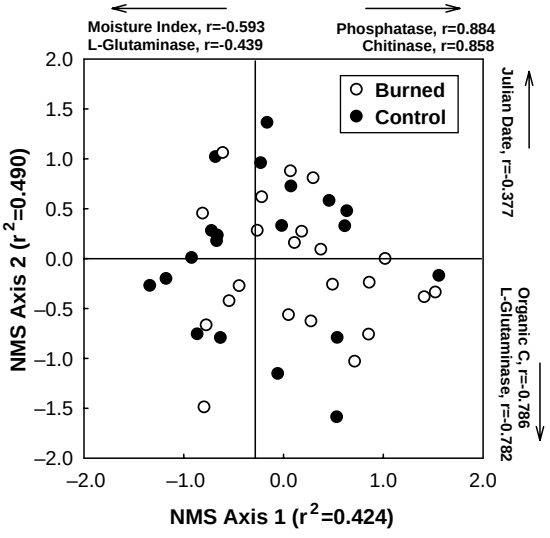

Fig. 6. Non-metric multidimensional scaling (NMS) ordination of sample plot means of five enzymes and soil organic C. The proportion of total variance explained by each composite axis is indicated. $N=42$.

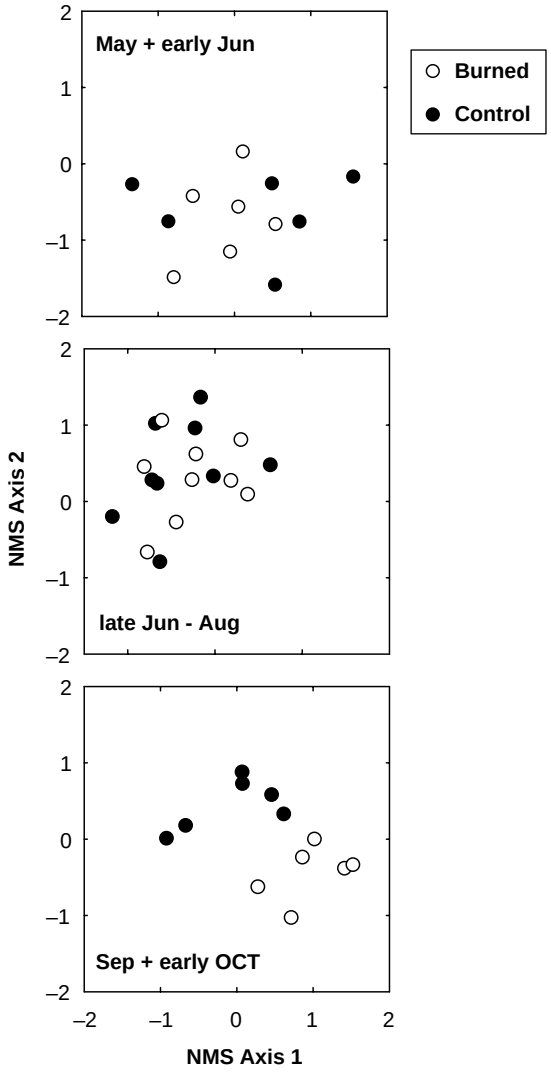

Fig. 7. NMS ordination sorted into three temporal subsets. The proportion of total variance explained by each composite axis is indicated. $N=42$.

and unburned plots in spring based on soil organic C and enzyme activities. Late season samples (i.e. September, October) ordinated in the center and the upper half of NMS Axis 2 (Fig. 7). The cluster of unburned plots were clearly separated from the cluster of burned plots, with the unburned plots generally higher on NMS Axis 2 and lower on NMS Axis 1. There was, therefore, a clear separation between ecosystem functional properties in burned and unburned plots based on late summer/early autumn samples.

4. Discussion

Studies that have documented seasonal variations in soil enzyme activity have sometimes attributed those variations to patterns of temperature and/or moisture; however, the specific seasonal patterns of activity have varied among enzymes, soil properties, and ecosystem types. The season variations in L-glutaminase we observed are consistent with the seasonal variations in acid phosphatase, β-glucosidase, and phosphodiesterase activity (i.e. greatest activity in spring with differences >50% by autumn) reported in a study of a beech (*Fagus sylvatica*) forest in Germany (Ratsin et al., 1998). In addition, Kang and Freeman (1999) reported maxima in early spring and minima in autumn in acid phosphatase activity that correlated closely with soil temperature, soil water content, and pH in swamp, fen, and bog habitats in UK. McClaugherty and Linkins (1990) observed that chitinase, laccase, and peroxidase activities in winter samples at 0 °C were 20–67% of those in autumn samples at 15 °C. Thus there is some evidence that the seasonal patterns of temperature and moisture typical of north temperate ecosystems can affect soil enzyme activity.

However, we did not observe seasonal effects on the activities of all of enzymes whose activity we measured, and other studies have also reported little seasonality in soil enzyme activity. For example, Dick et al. (1988) observed little seasonality in acid phosphatase or β-glucosidase activity in North American agricultural fields, and Bandick and Dick (1999) reported that β-glucosidase activity varied little in relation to soil moisture in similar systems. Finally, Bergstrom et al. (1998) observed that seasonal variations in β-glucosidase activity were small when compared to year-to-year variations.

The key to understanding seasonality in enzyme activity may be in the factors that regulate various enzyme systems. Chitinase and acid phosphatase are regulated by primarily microclimate and soil chemical factors, whereas lignocellulose degrading enzymes such as glucosidases and phenol oxidase are more regulated by substrate availability (Sinsabaugh et al., 1992, 1993). In our study sites, soil organic matter increases through the growing season even as soil moisture decreases; particularly in recently burned areas. Thus, it is logical that α-glucosidase and phenol oxidase would increase over the season while acid phosphatase, chitinase, and L-glutaminase would decrease.

Soil organic C content increased significantly in late summer and early autumn in the burned plots but not the unburned plots, and this was mirrored in significantly greater activity of acid phosphatase, chitinase, and phenol oxidase on a soil mass basis in burned than unburned plots. However, when enzyme activity was calculated on an organic matter basis, the fire-related differences in acid phosphatase and phenol oxidase activity disappeared. Thus, the apparent effects of fire on these two enzymes were, at least to some extent, a reflection of a change in substrate availability.

In a study of soil enzyme activity after annual and periodic fires over four years on enzyme activity in nearby forest sites, multiple fires resulted in a decrease in acid phosphatase and β-glucosidase activity and an increase in phenol oxidase activity (Boerner and Brinkman, 2003). We interpret the differences between these earlier results

and those we present in this study to be a function of fire intensity. The present study reports enzyme activities following a single, relatively cool fire whereas our earlier work considered the cumulative effects of multiple fires, most of which were considerably more intense than the one in the present study.

Support for this view comes from other long-term fire studies. Eivasi and Bryan (1996) reported that 45 years of annual and periodic prescribed fire in a Missouri oak-hickory forest resulted in significantly lowered acid phosphatase activity, β-glucosidase activity, and microbial biomass without significant change in pH or soil organic C. They attributed the decrease in microbial activity to changes in organic matter quality, not to changes in microclimate. In contrast, Aiwa et al. (1999) found that long-term burning at Konza Prairie; resulted in decreased microbial biomass and β-glucosidase activity but increased acid phosphatase activity. This is an intriguing result, as many studies have reported strong, positive correlations among acid phosphatase activity, β-glucosidase activity, and microbial biomass (e.g. Eivasi and Bayan, 1996; Kandeler and Eder, 1993; Nannipieri et al., 1983).

Our prior studies of the effects of fire on soil enzyme activity (Boerner et al., 2000; Boerner and Brinkman, 2003) have focused on variations related to landscape position and fire frequency/intensity, and have relied entirely on sampling each year at approximately the same time (late summer). We chose late summer for annual sampling to minimize the potential for Type I errors caused by what we expected to be greater short-term variability in weather, forest floor conditions, and microbial activity early in the growing season. In the study reported here, we did indeed observe greater variability in activity in all enzymes testing in the May and June samples than in the samples from later in the growing season.

NMS Ordination of the five enzymes and soil organic C revealed patterns among sample dates and fire treatments that correlated strongly with landscape position (measured as Integrated Moisture Index), organic C content, season, and L-glutaminase activity. Comparison of the positions of all of the sample plots in ordination space did not reveal a clear separation between burned and unburned sample plots. The same was true when the comparison was limited either to samples taken early in the growing season (May and early June) or to samples taken in the middle of the growing season (late June through August). In contrast, the clusters corresponding to samples taken in the latter part of the growing season (September and early October) did separate clearly in ordination space, primarily on the basis of L-glutaminase activity. Thus, when a suite of enzymes plus soil organic C were evaluated simultaneously, one would conclude that fire had no significant effect on soil enzyme activity unless (1) sampling was restricted to the last month of the growing season and (2) L-glutaminase was included in the suite of enzymes. This result, if confirmed by on-going studies with other enzyme systems, will underscore the need for understanding seasonality in soil processes before designing sampling protocols.

The use of enzyme profiles to assess soil quality and effects of management strategies is gaining considerable support. In a study of the effects of conservation tillage practices on agroecosystem sustainability, Bergstrom et al. (1998) concluded "[b]ecause of their sensitivity, ease, and low cost of measurement, soil enzyme activities may be very valuable for soil assessments related to sustainability." We endorse their view that soil enzyme activity profiles have great promise in this regard, but with the caution that understanding landscape and seasonal patterns of variation must be a prerequisite for the use of such indicators in assessment of management or restoration strategies.

Acknowledgements

This is publication number 60 of the Fire and Fire Surrogate (FFS) Project funded by the US Joint Fire Sciences Program. We thank Jianjun Huang, Philip Saksa, and Jessica Siders Kahler for assistance in the field and lab.

References

Aiwa, J.A., Dell, C.J., Rice, C.W., 1999. Changes in enzyme activities and microbial biomass of tallgrass prairie soils as related to burning and nitrogen fertilization. Soil Biology & Biochemistry 31, 769–777.

Allison, L.E., 1965. Organic carbon. In: Black, C.A., Evans, D.D., White, J.L., Ensminger, L.E., Clark, F.E. (Eds.), Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties. American Society for Agronomy, Madison, WI, pp. 1367–1378.

Bandick, A.K., Dick, R.P., 1999. Field management effects on soil enzyme activities. Soil Biology & Biochemistry 31, 1471–1479.

Bergstrom, D.W., Monreal, C.M., King, D.J., 1998. Sensitivity of soil enzyme activities to conservation practices. Soil Science Society of America Journal 62, 1286–1295.

Boerner, R.E.J., Brinkman, J.A., 2003. Fire frequency and soil enzyme activity in southern Ohio oak-hickory forests. Applied Soil Ecology 23, 137–146.

Boerner, R.E.J., Brinkman, J.A., 2004. Spatial, temporal, and restoration treatment effects on soil resources in Ohio hardwood forests, In: Yaussy, D.A. (Ed.), Proceedings of the 14th Central Hardwood Forest Conference. USDA Forest Service General Technical Report NE-316, Newtown Square, PA, pp. 241–254.

Boerner, R.E.J., Sutherland, E.K., 2003. Physiography, geology and soil classification, In: Sutherland, E.K., Hutchinson, T.F. (Eds.), Characteristics of Mixed Oak Forest Ecosystems in Southern Ohio Prior to the Reintroduction of Fire. USDA Forest Service, Northeastern Research Station General Technical Report NE-299, Newtown Square, PA, pp. 43–46.

Boerner, R.E.J., Decker, K.L.M., Sutherland, E.K., 2000. Prescribed burning effects on soil enzyme activity in a southern Ohio hardwood forest: a landscape-scale analysis. Soil Biology & Biochemistry 32, 899–908.

Decker, K.L.M., Boerner, R.E.J., Morris, S.J., 1999. Scale dependent patterns of soil enzyme activity in a forested landscape. Canadian Journal of Forest Research 29, 232–241.

Dick, R.P., 1994. Soil enzyme activities as indicators of soil quality. In: Doran, J.W., Coleman, D.C., Bezdicek, D.F., Stewart, B.A. (Eds.), Soil Enzymes. Soil Science Society of America, Madison, WI, pp. 107–124.

Dick, W.A., Tabatabai, W.A., 1992. Significance and potential use of soil enzymes. In: Metting, F.B. (Ed.), Soil Microbial Ecology. Marcel Decker, NY, pp. 95–130.

Dick, R.P., Rasmussen, P.E., Herle, E.A., 1988. Influence of long term residue management on soil enzyme activities in relation to soil chemical properties of a wheat-fallow system. Biology and Fertility of Soils 6, 158–164.

Eivasi, F., Bayan, M.R., 1996. Effects of long-term prescribed burning on the activity of selected soil enzymes in an oak-hickory forest. Canadian Journal of Forest Research 26, 1799–1804.

Frankenberger, W.T., Tabatabai, M.A., 1991a. L-glutaminase activity of soils. Soil Biology & Biochemistry 23, 869–874.

Frankenberger, W.T., Tabatabai, M.A., 1991b. Factors affecting L-glutaminase activity in soils. Soil Biology & Biochemistry 23, 875–879.

Hamilton, C.M., Sims, J.T., 1995. Nitrogen and phosphorus availability in enriched, palletized poultry litters. Journal of Sustainable Agriculture 5, 115–132.

Iverson, L.R., Dale, M.E., Scott, C.T., Prasad, A., 1997. A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (USA). Landscape Ecology 12, 331–348.

Kandeler, E., Eder, G., 1993. Effects of cattle slurry in grasslands on microbial biomass and on activities of various enzymes. Biology and Fertility of Soils 16, 249–254.

Kang, H., Freeman, C., 1999. Phosphatase and arylsulfatase activities in wetland soils: annual variation and controlling factors. Soil Biology & Biochemistry 31, 449–454.

McClaugherty, C.A., Linkins, A.E., 1990. Temperature responses of enzymes in two forest soils. Soil Biology & Biochemistry 22, 29–33.

Morris, S.J., 1999. Spatial distribution of fungal and bacterial biomass in southern Ohio hardwood forest soils: fine scale variability and microscale patterns. Soil Biology & Biochemistry 31, 1375–1386.

Nannipieri, P., Muccini, L., Ciardi, C., 1983. Microbial biomass and enzyme activities: production and persistence. Soil Biology & Biochemistry 15, 679–685.

Ratsin, N., Rosenplänter, K., Hüttermann, A., 1998. Seasonal variation of enzyme activity and their dependence on certain soil factors in a beech forest soil. Soil Biology & Biochemistry 20, 637–642.

Riebold, R.J., 1971. The early history of wildfires and prescribed burning. In: Proceedings, Prescribed Burning Symposium. USDA Forest Service, Asheville, NC, pp. 11–19.

Saa, A., Trasar-Cepeda, M.C., Gil-Sotres, F., Carballas, T., 1993. Changes in soil phosphorus and acid phosphatase activity immediately following forest fires. Soil Biology & Biochemistry 25, 1223–1230.

SAS, 1995.Anon., 1995. Statistical Analysis System (SAS): User's Guide. On-line documentation. SAS Institute, Cary, NC.

Sinsabaugh, R.L., Findlay, S., 1995. Microbial production, enzyme activity, and carbon turnover in surface sediments of the Hudson River estuary. Microbial Ecology 30, 127–141.

Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., Rayburn, L., Repert, D., Weiland, T., 1992. Wood decomposition in a first order watershed: mass loss as a function of exoenzyme activity. Soil Biology & Biochemistry 24, 743–749.

Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., McClaugherty, C.A., Rayburn, L., Weiland, T., 1993. Wood decomposition: nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. Ecology 74, 1586–1593.

Stewart-Oaten, A., Murdoch, W.W., 1986. Environmental impact assessment: 'pseudoreplication' in time?. Ecology 67, 929–940.

Sutherland, E.K., Hutchinson, T.F., (Eds.), 2003. Characteristics of Mixed Oak Forest Ecosystems in Southern Ohio prior to the Reintroduction of Fire. USDA Forest Service, Northeastern Research Station. General Technical Report NE-299, Newtown Square, PA, 159p.

Tabatabai, M.A., 1982. Soil enzymes. In: Page, A.L., Miller, R.H., Kenney, D.R. (Eds.), Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties, second ed. American Society for Agronomy, Madison, WI, pp. 903–947.

Underwood, A.J., 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecological Applications 4, 3–15.